THE MIGRATORY HABITS OF THE MARINE GRIBBLE LIMNORIA TRIPUNCTATA MENZIES IN SAN DIEGO HARBOR, CALIFORNIA [1, 2]

MARTIN W. JOHNSON AND ROBERT J. MENZIES

Scripps Institution of Oceanography of the University of California, La Jolla, California

The isopod gribble *Limnoria* is a serious wood-boring pest in nearly all tropical, temperate, and boreal harbors where contamination has been established and where salinities are not markedly reduced by influx of fresh water. Typical examples of the ravishes of one or more species of this borer are offered by the findings of the San Francisco Bay Marine Piling Committee (Kofoid and Miller, 1927). During that survey only *Limnoria lignorum* (Rathke) was recognized, but Holthuis (1949) has shown that the species *L. quadripunctata* described by him as new was present in the area and had been confused with *L. lignorum*. Actually two species exist in San Francisco Bay, neither of which is *lignorum* (Menzies and Mohr, 1952).

Examination of collections from the San Diego region and elsewhere in California led Menzies (1951) to establish yet another species, *L. tripunctata* which has hitherto also been confused with *L. lignorum*.

Along the west coast of North America the geographic ranges of the three species of wood-boring *Limnoria* have been established as follows (Menzies, in manuscript): *Limnoria lignorum* (Rathke); Alaska to Point Arena, California. *Limnoria quadripunctata* Holthuis; California (41° N) to San Diego Bay. *Limnoria tripunctata* Menzies; warm parts of San Francisco Bay to Mazatlan, Mexico.

The seasonal activities of *L. lignorum* were studied at Friday Harbor, Washington, by Johnson (1935) who found that that species undergoes a pronounced seasonal swimming migration at which time new wood is attacked mainly during early spring. Sömme (1940) confirmed this type of activity for the same species in Norway and reported that a survey by Kramp in 1927 showed similar activity in Danish waters. Kramp's report, published in a Danish engineering journal, has escaped the attention of biologists in other parts of the world. He gives no figures of relative abundance or intensity of attack by *Limnoria lignorum* on new test blocks but states that at Hirtshals, Denmark, there was a pronounced maximum of attack in April. He concludes that the attacks result from periodic swarming of mainly adult individuals. Following the April swarming, the attacks occur in diminishing intensity during the summer.

It is of practical interest to know to what extent the findings relative to the northern species *L. lignorum* can be generally applied to the other species. With this in mind, the present study was designed to test *L. tripunctata*, a species of world-wide distribution in southern waters and the only one found in San Diego Bay.

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PROCEDURE

As a means of determining the migratory habits of *Limnoria tripunctata,* wooden test blocks were suspended freely in the water in the immediate vicinity of piling known to be heavily infested with *Limnoria.*

The test blocks consisted of 5 × 8 × 1 inch Douglas fir which provided about 106 sq. in. (684 cm.^{2}) of surface that could be examined by means of a low-power binocular microscope. After having been soaked in sea water free of borers for a period of 14 days, the blocks were attached to a rope line or stainless steel wire which was suspended from the pier and held taut by a concrete weight attached to the lower end, such that the weight hung free of the bottom. Test blocks thus rigged were located about one foot from infested piling so that they could be reached only by swimming migrating animals.

Two test stations were established in San Diego Bay: Station "A" at the U. S. Naval target repair base at Point Loma and Station "B" at the Johnson and Western Pier well within the bay near the Coronado ferry landing. Owing to reconstruction and repair there was some interruption at each station. The vertical position of the blocks and approximate days of exposure for each are given in Table I.

TABLE I

Position and exposure of test blocks

Station A

Aug. 12, '52–Aug. 13, '53		Aug. 13, '53–Feb. 15, '54		Apr. 14, '54–Mar. 14, '55	
Position of blocks	Days of exposure	Position of blocks	Days of exposure	Position of blocks	Days of exposure
Floating*	60				
Floating	30	Floating	30	Floating	30
6 ft. from bottom	30	6 ft. from bottom	60	6 ft. from bottom	60
4 ft. from bottom	30	4 ft. from bottom	90	4 ft. from bottom	90

* Zero tide datum is approximately 14.6 feet above bottom. The mean tidal range was approximately 4 feet.

Station B

Aug. 15, 1952–Aug. 13, 1953		Feb. 15, 1954–Mar. 14, 1955	
Position of blocks	Days of exposure	Position of blocks	Days of exposure
Floating**	30	5 ft. from bottom	30
2 ft. from bottom	30	4 ft. from bottom	60
		3 ft. from bottom	90
		2 ft. from bottom	120

** Zero tide datum is approximately 9 feet above bottom. Tidal range same as for Station A.

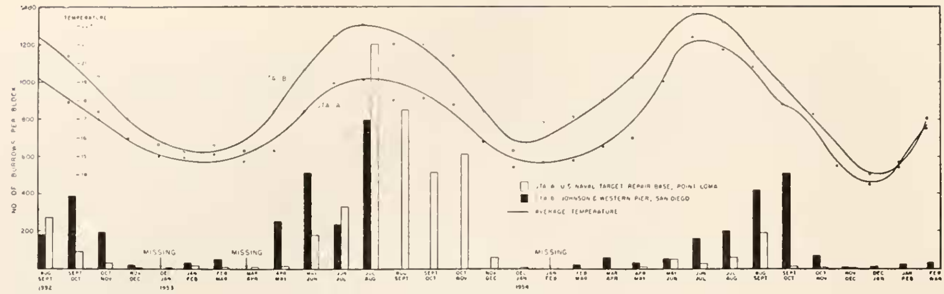

FIGURE 1. *Limnoria tripunctata.* Seasonal attack on test blocks exposed for successive 30-day intervals at Stations A and B, San Diego Bay from August, 1952 to March 14, 1955. Seasonal temperature included.

The intensity of settlement or attack on the blocks for a given period is taken to represent the intensity of migration for the period. It is determined by counting the number of burrows in the surface of the wood. Usually there are two animals, male and female, in each of the deeper burrows.

Surface temperature of the water was taken once each month at each station except for the period 15 August 1953 to 7 May 1954 when a continuous temperature recorder was in operation near Station A. Salinities in San Diego Bay fluctuate but little. The mean annual value is about 33.6‰.

Requirements for a study of this nature are: (1) nearby ample source of gribble infestation; (2) little or no interference resulting from repair or removal of piling; (3) safety from ship action, heavy seas or pilferage; (4) absence of adverse conditions due to low dissolved oxygen or low salinity.

These requirements were well met but for the already mentioned changes due to pier repair.

RESULTS

Seasonal Migrations

An examination of the severity of attack on the test blocks reveals that migration occurs to a greater or lesser degree throughout the year, but as in *L. lignorum,* there was each year a period of pronounced increase in migratory activity. In migrating the animals swim freely and a special preliminary study designed to reveal diurnal behavior in nature indicates that the greatest swimming activity takes place at night.

In Figure 1 is shown graphically the monthly seasonal fluctuations in migration between Aug. 12, 1952 and March 14, 1955 inclusive. The data used in compiling the figure were derived from the blocks submerged for successive 30-day periods with omissions as noted. Other periods of submergence, especially the 60-day periods, provided corroborative data on season of attack (Fig. 5) but the longer periods of submergence were designed mainly to provide information on rate of growth, sexual condition and reproduction.

The test blocks that were in place for 30-day periods beginning August 12, 1952, apparently caught mainly the declining portion of that year's migration.

In 1953 at Station A there was a period of active migration which extended from about the middle of May to the middle of November with a maximum during July–

August. This was also the peak 30-day period for Station B. This station was abandoned in August, 1953 when it was apparent that both stations at the various depth levels were showing a similar migratory picture; however, it was re-established when the reconstruction of piles at Station A forced a temporary abandonment of that station in January, 1954. By April, 1954 both stations were again studied until the completion of this phase of the work in March, 1955.

From the time of re-establishing of Station A in April, 1954, the attack on the blocks was relatively light but with a definite maximum occurring this time in August–September. The lighter attack may be attributed to a diminished source of infection as a result of replacement of infested piling, etc., with new pressure-treated creosoted timbers which left only a nearby infested stub and doubtless other undetected submerged wood, and some more distant infested structures. This also explains the low migratory figure shown in Figure 5 for the second year.

The main season of attack at Station B appears to be during August and September after which it diminishes rapidly to the low winter level.

The seasons of active attack on the blocks roughly coincide at the two stations, but it appears to have continued somewhat later at Station B in 1952 and began slightly earlier in 1953. The same trend is suggested in 1954. This difference may be correlated with the temperature. From Figure 1 it will be noted that a higher temperature prevailed throughout the year at Station B.

It has commonly been reported that the attack by *Limnoria lignorum* is not so great on floating or shallowly placed test blocks as it is on deeper blocks or near the bottom (Johnson and Miller, 1935; Sömme, 1940; Black and Elsey, 1948). This may be a factor of considerable importance in the relative rate of deterioration of floating or driven structures. However, our data from *Limnoria tripunctata* indicate that it shows no marked preference with respect to depth of settlement.

In order to better understand the migratory activity of *Limnoria* in light of its population biology an analysis was made of the seasonal composition of the population from the piling and from the test blocks. For this purpose the animals were studied as to size and, in the older specimens, also as to sex and reproductive condition.

Accurate measurements of the body length of *Limnoria* are usually difficult to obtain because of the natural tendency of the animals to assume a strongly bent position or for the segments to become more or less telescoped depending upon the type of preservative used or upon other factors such as ovarial development or injury. A practical substitute is therefore here made by using the pleotelson width at its widest point as an index of size. This has the advantage that we here deal with a flat rigid structure (the last segment of the body) that is not readily distorted. It has the further advantage that the size of animals in shallow burrows may often be determined without removing them from the burrow, and also the size of exuviae can be determined by this one fragment of the generally disarticulated cast.

Ten size categories can be established more or less clearly based on the width of the pleotelson.

In the literature dealing with *Limnoria*, the size index given is always in length; hence it will be useful here to provide Table II giving conversions of pleotelson widths to body lengths for the ten groups.

TABLE II

Limnoria tripunctata. Pleotelson width to body length. 180 animals measured

Size class	Mean pleotelson width, mm.	Body length, mm.		Remarks
		♂	♀	
1	0.24–0.26	0.8–1.2		Young lacking seventh pair of pereiopods
2	0.28–0.33	1.0–1.6		Young lacking seventh pair of pereiopods
3	0.35–0.40	1.1–1.6		Young with underdeveloped seventh pair of pereiopods
4	0.42–0.46	1.5–2.2	1.5–1.5	Sexual maturity reached by males
5	0.48–0.53	1.7–2.2	1.9–3.0	Females develop oostegites
6	0.55–0.60	2.1–3.0	1.8–3.0	Females become gravid
7	0.61–0.67	2.0–3.3	2.6–3.5	Includes majority of reproductive individuals, especially the females
8	0.69–0.74	2.5–3.4	3.0–3.8	Includes majority of reproductive individuals, especially the females
9	0.76–0.81	2.5–3.4	2.7–3.5	Includes majority of reproductive individuals, especially the females
10	0.82–0.86	2.5–3.2	2.5–3.8	Only few reach this size

An analysis of the population composition of a one-month test block and of old piling on the same date are given respectively in Tables III and IV. The results are quite typical, but for piling populations, there may be considerable variation in samples of one square inch in size taken adjacently in the same pile; hence, in most instances, counts were made in duplicate or triplicate.

A comparison of the percentage composition of the populations shown in Tables III and IV reveals that over 97% of the migrants are sexually mature animals of fairly large size, whereas on the piling, only about 28% are sexually mature, over 50% are newly hatched or immature animals, and 19% intermediate.

Analyses of piling samples taken monthly are given in Table V where the percentage composition of size classes are given and the mean calculated for three-month periods. Thus the variations are smoothed out to give seasonal means for

TABLE III

Limnoria tripunctata. Migrant population, Station A, Sept. 13, 1952. Numbers in size class, maturity, sex and per cent of total population (164) in test block of each month exposure

Size class	Immature	♀ (?) Young	♀ with oostegites	♀ gravid	♂
3	1				
4		2			1
5		1			16
6					12
7			21	7	25
8			12	10	11
9			18	11	10
10			2	2	2
% of Total	0.60	1.81	32.29	18.26	46.90

TABLE IV

Limnoria tripunctata. Piling population, Station A, Sept. 13, 1952. Numbers in size class, maturity, sex and per cent of total population in one square inch sample of infested wood with a total of 432 animals

Size class	7th pereiopod lacking	Immature	♀ (?) Young	♀ with oostegites	♀ gravid	♂
1	83					
2	36	39				
3		69	39			
4			39			8
5			5	4		10
6				10		7
7				7	13	23
8				8	10	7
9				4	7	4
% of Total	27.54	24.99	19.19	7.62	6.93	13.64

spring, summer, autumn, and winter. From this it appears that the piling population remains rather constant in its composition with some preponderance of the youngest class during the migratory months (June–November) and of the middle group during the winter (December–February) and relatively more adults in the spring (March–May) prior to heavy migration.

In the test block population presented in Table III, there is a slight predominance of females over males. It appears, however, from analyses of many block

TABLE V

Limnoria tripunctata. The mean percentage of size composition for monthly and seasonal periods for piling populations, 1952–1953

Size class	Spring			Seasonal mean	Summer			Seasonal mean
	March	April	May		June	July	August	
1–3	16	65.5	34	38.5	31.5	48	44	41.3
4–7	53.8	19.5	40.3	38	48	43.5	35	42.3
8–10	33.7	20	29	27.5	20.5	8.5	21	16.7
No. examined	403	783	792		545	449	300	
Size class	Autumn			Seasonal mean	Winter			Seasonal mean
	Sept.	Oct.	Nov.		Dec.	Jan.	Feb.	
1–3	69	34	47.5	50.3	17	53	33	34.3
4–7	16	51	40.3	35.8	63.5	34	54	50.7
8–10	15	15	12.3	14.1	19.6	13	13	15.2
No. examined	449	328	1282		557	153	44	

and piling samples, that the ratio of males to females on the piling is on an average about 1 to 1 for sexually mature specimens, whereas on test blocks it is often 1.3 to 1. This suggests that the males have a greater tendency to migrate than do the females, especially the younger females. Mating occurs after migration, the females becoming gravid some time after they have become established on the test block. This is evidenced by observations that (1) gravid females were found only in the longest, hence oldest burrows of the thirty-day test blocks, (2) here they occupied the blind end of the burrow while the male occupied the open end, (3) no gravid females were observed to occupy a burrow singly. This is in accord with the conclusions regarding the breeding habits of *Limnoria lignorum* (Kramp, 1927; Johnson, 1935; Sömme, 1940). Further evidence substantiating the opinion that migration precedes fertilization is found in Menzies' (1954) report which shows that females lack a sperm storage organ and the sperm produced by the male are relatively few in number and not grouped into spermatophores.

Sperm were found only in the oviduct of females which were moulting prior to deposition of eggs into the brood pouch. None were found in virgin or gravid females. Copulation probably precedes each brood production.

Factors Influencing Migration

Temperature

As shown in Figures 1 and 5 for *Limnoria tripunctata* and Figure 2 for *L. lignorum,* there is a certain correlation between the water temperature and the intensity of migration as indicated by severity of attack on the test pieces. The figures do, however, show a sharp difference in the maximum migratory period of the two species as related to the temperature curve and season of the year. *L. lignorum* reaches a peak of migratory activity on a rising temperature whereas *L. tripunctata* follows more nearly the seasonal trend of temperature with some tendency to lag behind. However, it should be pointed out that while the above appears to be typical for *L. lignorum,* at widely separated areas, data from Tromsösund, Norway, show a period of greatest migratory activity on a falling temperature. Sömme (1940) concluded that the season of migration varied with hydrographic conditions; hence each locality requires special investigation to determine the season of maximum attack on new wood. In a survey designed mainly to test the depth of attack in British Columbia waters, Black and Elsey (1948) indicate some variation in season of attack by *L. lignorum.* However, their data show that in areas such as Williams Head, Bentinick Island, and Esquimalt, which are not seriously affected by dilution, the main attack was during spring. The data used in Figure 2 A and B are derived from analysis of test blocks kindly provided us by the William F. Clapp Laboratories.

These differences in the two species may arise from specific differences in temperature requirements. Temperature *per se* may, however, not be the immediate cause of migration in either species of *Limnoria.* It is perhaps mediated through its effect on the rate of other biological activities such as growth, attainment of sexual maturity, and reproduction. Seasonal increases in these rates must lead to population pressure which is more acute at some seasons than at others.

Population pressure

In the study of *L. lignorum* at Friday Harbor (Johnson, 1935), it was hypothesized that migration results from overcrowding and approach of sexual maturity. Overcrowding is, of course, closely dependent upon the nature and availability of food supply and living space. *Limnoria*, like other wood borers, is unique in that it eats the substratum on which it lives. Limits to size and growth of the population are therefore set by the area of available wood. When conditions become intolerable due to population pressure, either a migratory movement must take place or the ratio of reproduction and growth to mortality must change. That the first takes place, we know, and there is some evidence also of the latter. The rate of growth, age of attainment of sexual maturity, and fecundity are then of prime importance in an understanding of migration.

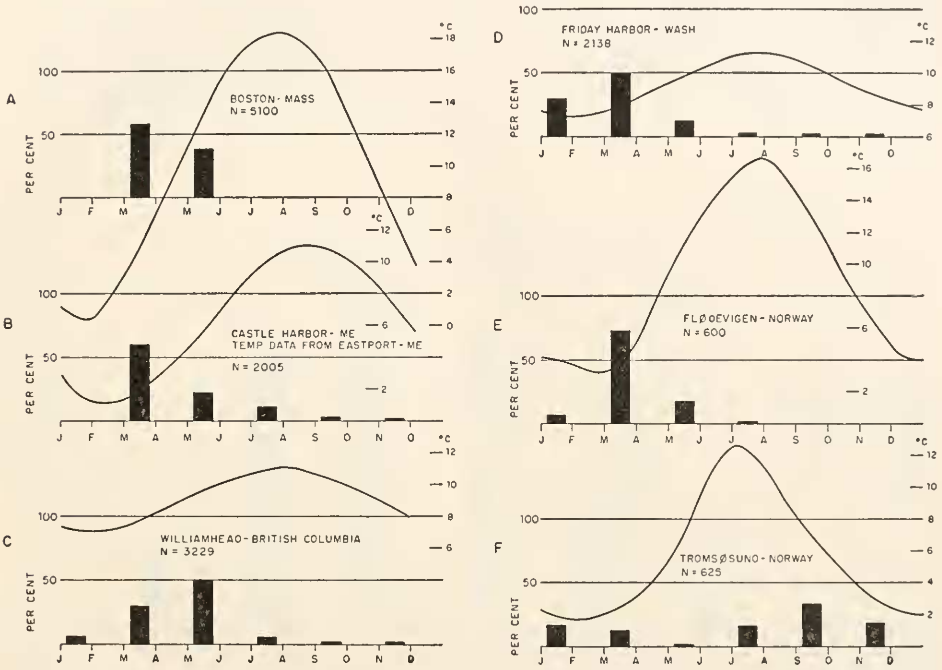

FIGURE 2. *Limnoria lignorum.* Percentage of seasonal attack in bimonthly periods in various localities. A and B data from William F. Clapp Laboratories; C from Black and Elsey, 1948; D from Johnson, 1935; E and F from Sömme, 1940. N = Yearly sum of animals on test blocks.

Fecundity Related to Overcrowding

That there is a reduction of fecundity in a crowded population is indicated in Table VI. Here it is apparent that with increased size of the female, as shown by pleotelson width, there is also an increase in the number of eggs produced. This relationship is more evident for the test-block than for the piling population. It will be noted also that the brood size of piling populations remains approximately one-half the size of that of the migrant population irrespective of size increase in the female. Thus it appears that an increased population density influences the brood size so that the rate at which young are added to a dense population may be only about one-half that at which they are added to a sparse population with plenty of wood for expansion. However, even with this adjustment, the population pressure must increase as the living space diminishes.

Fecundity Related to Temperature

The rate of development of eggs in the ovaries appears to be temperature-dependent. Brood-bearing females were found at Station A on test blocks which had been submerged for 30-day intervals all months of the year except the winter. In July and August, 1954, a brood was produced and hatched in 30 days at a temperature near 20.8° C. Test blocks submerged for 60 days showed gravid females

TABLE VI

Limnoria tripunctata. Comparison of brood size with size in females from old wharf piles and from 30-day test blocks

Size class	Piling			Test blocks		
	No./brood		No. gravid ♀♀ examined	No./brood		No. gravid ♀♀ examined
	Mean	Range		Mean	Range	
6	4.6	1–6	11	—	—	None found
7	5.8	1–12	25	8.9	4–18	35
8	4.0	1–12	28	10.8	1–18	79
9	5.1	1–12	34	12.4	1–22	95
10	7.0	1–12	3	10.5	4–21	21

throughout the year and hatched young most months of the year except during the spring of 1953 and in January and February, 1954. Station B yielded similar results for the 30-day exposures except that a brood was produced and hatched in less than 30 days in April and May (mean temperature 19.5° C.). The deposition of eggs and hatching of broods did not occur within 60 days at Station A during the winter or spring months of 1953–54 when temperatures ranged from 14.8 to 15.8° C. This suggests that with a temperature difference of only 5° C., it takes about twice as long to produce and incubate young during winter as it does during the summer.

It was observed that at least during the summer months, females with hatched young also had ripe ovaries and could incubate another brood soon after the emergence of the first batch from the pouch. Frequently young and their secondary or lateral burrows were observed in a burrow of a gravid female. In the test blocks exposed for three-month periods, the following maximum numbers of broods were observed: Station A, mid-November, 1953–mid-February, 1954 (mean temperature 14.8° C.) one brood; mid-July–mid-October, 1954 (mean temperature 20.6° C.) three broods; mid-August–mid-November, 1954 (mean temperature 17.4° C.) two broods; Station B, mid-February–mid-May, 1953 (mean temperature 18.6° C.) two broods. Using size as a criterion, it appears that migrant females may have produced one or two broods prior to migration. This is indicated in Figure 3 which should be coordinated with Table II showing that females may become gravid in size class 6. Females in size class 10, the largest, were found only in migrant populations. Although migrants must frequently land on already heavily infested wood, the relative absence of the large females probably indicates that few, if any, re-establish themselves in dense populations. Thus the implication is that migration is largely an urge to seek less crowded conditions. Analysis of the population forming the basis of Figure 3 shows also that the summer and fall gravid migrants

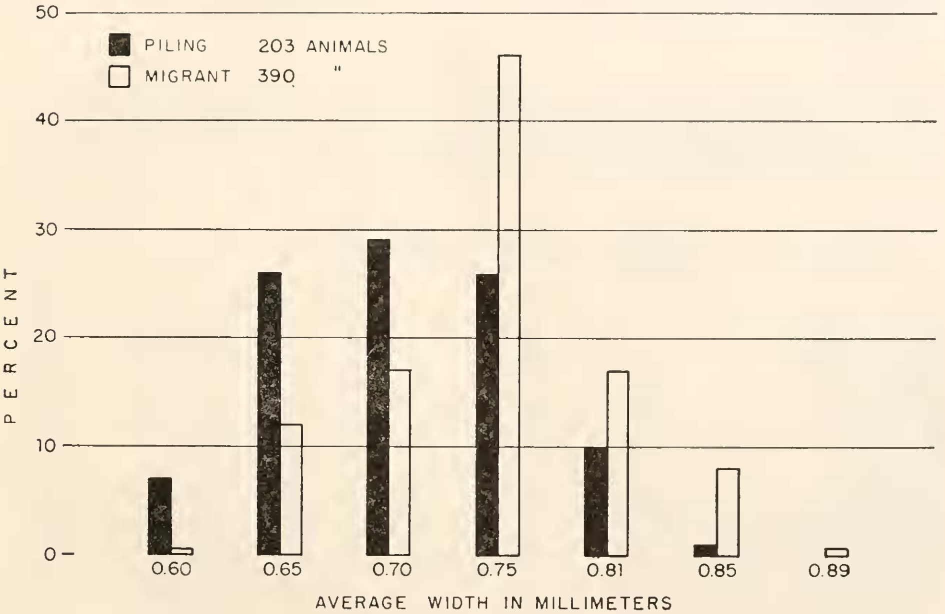

FIGURE 3. *Limnoria tripunctata*. Percentage size composition of gravid female populations.

average 0.04 mm. smaller than those of other seasons and the gravid females from piling average 0.05 mm. smaller, thus indicating that sexual maturity is reached at a smaller size (hence more rapidly) during the warmer months.

That reproduction in *Limnoria* is influenced seasonally by temperature is further indicated by a study of the "gravidity" which may be defined as the per cent of gravid females among the adult females occurring at any time in a piling population of maximum density (Table VII).

From Table VII, it seems evident that gravidity for this species reaches its peak somewhere between 17° and 19° C., declining at temperatures above and below these values. Gravidity appears to double between 14° and 18° C. In laboratory cultures only 28% became gravid at 24° C. The broods of specimens kept at 34° C. deteriorated, suggesting that such high temperatures may unfavorably affect brood production. At Beaufort, N. C., Coker (1923) reported no gravid females at

10° C. Mawatari (1950) reports that temperatures of 2–6° C. are lethal to *Limnoria lignorum* (probably *L. tripunctata*).

In contrast the northern species *Limnoria lignorum* appears to reach its peak gravidity at about 10° C., based on data from Johnson (1935). These data (assuming a 50-50 ratio of males to females) indicate that with environmental temperatures from 7.9° to 11.1° C. the gravidity figures varied from 22% to 79%, whereas at 7.5° C., the lowest temperature encountered, it was down to 14%. Sömme (1940) reports that *Limnoria* ceases to produce eggs at temperatures of 0° C. and below. In experiments she observed that the brood of a gravid female kept at 24.7° C. failed to develop after five days; at 14.8° C. and 6.3° C. development was apparently normal but at the lower temperature about twice the time was required as at an average of 13° C.

TABLE VII

Limnoria tripunctata. Seasonal gravidity (per cent gravid females of sexually mature females, 50/50 sex ratio assumed) in piling populations, Station A, 1952–1953. Figures based on gross size-class analyses of two to three one square inch samples of wood per month

Month sample collected	Mature animals of both sexes examined	Total females	Gravid females	% Gravid	Temperature °C.	
					Range	Approx. mean
January, 1953	96	48	6	12	15.5–14.8	15
February, 1953	124	62	34	55	14.8–14.6	15
March, 1953	289	44	83	57	14.6–15.0	15
April, 1953	109	54	31	57	15.0–15.5	15
May, 1953	220	110	68	62	15.5–16.3	16
June, 1953	133	66	53	80	16.3–18.3	17
July, 1953	44	22	12	55	18.3–19.2	18
August, 1953	53	26	28	100*	19.2–19.3	19
September, 1952	121	60	42	70	18.5–17.4	18
October, 1952	57	28	17	60	17.4–16.2	16
November, 1952	154	77	55	71	16.2–15.4	16
December, 1952	104	52	2	4	15.4–14.8	15

* In this case there were obviously more females than males in the sample.

Individual and population growth

The habits and life history peculiar to *Limnoria* make it possible to determine the growth rates of individuals and to follow the development of one or more broods in nature. To accomplish this, the test block (habitat) must have remained in the water a sufficiently long time to allow the migrants to incubate their broods and for the young to grow, but not so long that young of a second generation or new migrants confuse the picture. Development is direct and when the young emerge from the brood pouch, they immediately construct their own burrows within the walls of the parent burrow. The old female followed by the male continues burrowing deeper into the wood, so that subsequent broods released are separated more or less clearly from the previously released brood.

Thus up to the time that they may desert their burrows or have burrowed too far from the parent burrow, the young produced on the block can readily be distinguished from young which might have migrated to the block. Even specimens which have become sexually mature, and no longer associated with the parent burrow can usually be distinguished from sexually mature young migrants to the blocks because they occur in significantly larger numbers than do the young (small) migrants.

Rate of Growth.

The growth rate of *Limnoria tripunctata* was determined by culturing individuals in the laboratory and from measurements of the growth of young on test blocks for two-, three-, and four-month intervals. The maximum growth rate seasonally as found in test block exposures is shown in Figure 4. An evident feature is the

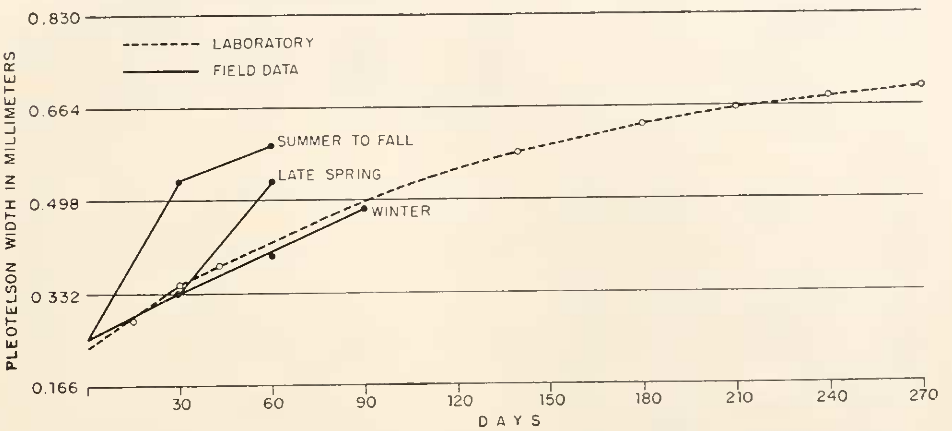

FIGURE 4. *Limnoria tripunctata.* Individual growth rate at different seasons: late spring, average temperature 19° C.; summer to fall, average temperature 22° C.; winter, average temperature 15° C.; laboratory culture average temperature 15° C. Measurements in field are from broods hatched on test blocks, those in laboratory, from individual specimens.

seasonal difference in growth rate of the young. Those emerging in winter require roughly twice as long to reach size class 5 (with 0.48–0.53 mm. pleotelson width) as do the spring young, and three times as long as the summer young. Thus increased crowding from growth of individual animals (distinguished from increased crowding resulting from addition of new individuals) would be greatest during spring and summer.

Population Growth.

Some idea can be had of the population growth by direct observation of the number and size of broods produced by migrant females during different portions of the year, namely on test blocks that were in place for successive 2-, 3- and 4-month periods throughout the year. In Table VIII summaries and calculations of probable annual rate of reproduction have been made, based on number of young observed in these 2- to 4-month periods.

Data from the test blocks show that a brood may be produced in a minimum of 25 days. The three- and four-month exposures indicate, however, that only one brood is produced during the winter, possibly three during the summer and at most only two during spring and fall. Thus a maximum of eight broods could conceivably result if a female can continue to produce successive broods at this rate. It has, however, been possible to follow the performance of individual females through a maximum of only three successive broods. Hence, it is not known whether or not a female that has produced three broods during the season of maxi-

TABLE VIII

Limnoria tripunctata. Rate of production of young based on observed values for test block populations

Station	Duration of test block exposure	Dates of exposure	Total number of months	Number of young found per 100 mature females	Raw monthly rate	Adjusted* monthly rate	Adjusted* annual rate
A	2 months	Aug. 1952–Oct. 1953	12	380	31.6	63.2	758
A	2 months	Oct. 1953–Dec. 1954	12	717	59.7	119.4	1433
B	2 months	Feb. 1954–Feb. 1955	12	619	51.6	103.2	1238
A	3 months	April 1954–Jan. 1955	9	1009	112.1	149.1	1789
B	3 months	Feb. 1954–Jan. 1955	9	1251	139.0	185.3	2224
B	4 months	Feb. 1954–Feb. 1955	12	1585	132.0	165.0	1980
					Average annual rate		1570

* In order to approach the reproductive continuity that must occur on piling, one-month incubation time is allowed. Raw monthly rate on blocks of 2-month exposure are accordingly doubled, those of 3- and 4-month exposures are increased by ⅓ and ¼ of raw rate, respectively.

mum production will continue to produce additional broods at the reduced rate at other seasons. Therefore, extrapolations must be considered with caution. Assuming an annual rate of eight broods with an average of 10 young per brood (Table VI) 100 females might produce a maximum of 8000 young. However, not all females in a population are gravid at any one time. The gravidity may be close to 100% during the mid-summer but drops as low as 4% during the winter (Table VII). An approximate mean gravidity for the year might be near 60% which would allow 100 females to produce only 4800 young per year at the rate shown for test board populations. Females in old piling populations appear to produce only about ½ this figure since their average brood size is only 5.

If the average annual realized reproductive performance of 100 sexually mature females is 1570 young as shown in Table VIII, the difference between this figure and the reproductive potential based on number and size of brood suggests the annual mortality on test blocks.

The reproductive rate given above may appear low compared with the potentialities suggested for *Limnoria lignorum* by Kramp (1927) who indicated four broods of 20–30 eggs per female per year. He, however, did not investigate the relative number of young resulting on the test blocks. Hence, no allowance was made for mortality. In Japan Shiino (1950) found only 1–12 eggs produced by *L. lignorum* (*tripunctata?*).

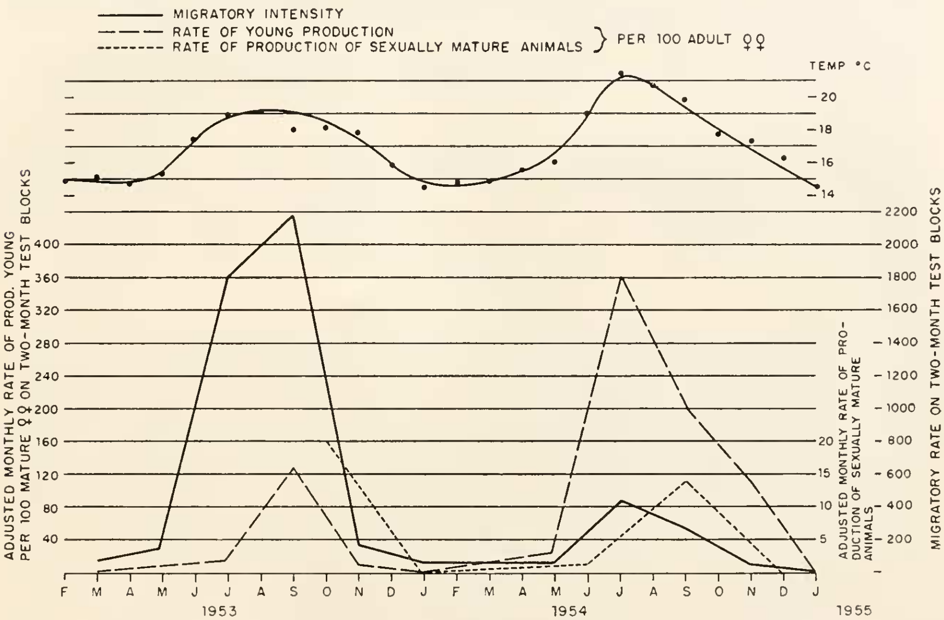

FIGURE 5. *Limnoria tripunctata.* The relationship between monthly production rates and migration in two-month periods, Station A, San Diego Bay.

The relationship between monthly production rate and migration in San Diego Bay is shown graphically in Figure 5. Interpolated to the piling, these data indicate that a marked increase would have occurred there during the months of maximal migration.

SUMMARY

1. *L. tripunctata* undergoes a definite seasonal migratory period which reaches its height approximately during the season of highest water temperatures. This differs from the earlier migratory season usually shown for *L. lignorum.*

2. The attack on new wood is about equally severe on floating and submerged blocks.

3. A comparison of the percentage composition of the 30-day test-block populations shows that about 97% of the migrants are sexually mature animals as con-

trasted with piling populations where 50% consisted of newly hatched immature animals and only about 28% sexually mature. The piling population remains fairly constant in its composition.

4. None of the females is gravid at the time of migration. Pairing takes place after establishment on the test blocks.

5. As with *L. lignorum* the factors influencing migration are probably a combination of approach to a reproductive phase and population pressure due to overcrowding in old established populations.

6. Water temperature is important in influencing migration in that the higher temperatures hasten the rate of growth and attainment of sexual maturity, production of eggs, and shorten the incubation period. Gravidity (per cent gravid females) in *L. tripunctata* evidently reaches its peak between 17° and 19° C. as contrasted with about 10° C. for *L. lignorum*.

7. The brood size of piling populations is about ½ that found in uncrowded test-block populations.

8. A single female probably produced three or more broods during the year.

9. Using size as a criterion, most migrant females appear to have produced a brood prior to migration.

10. In extrapolating the test-block data to the piling populations, there is indicated a marked population increase during the months of maximal migration.

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